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Skull anatomy and Comparative Cranial Osteology of *Eublepharis angramainyu* (Sauria: Eublepharidae) and *Asaccuselisae* (Sauria: Phyllodactylidae)

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ABSTRACT

The skull of the poorly known *Eublepharis angramainyu* (eyelidgecko) is described and compared with the skull of *Asaccus elisae* (a leaf-toed gecko). We provide a detailed description of the cranial osteology, lower jaw and dentition of *Eublepharis angramainyu* (Eublepharidae) and *Asaccuselisae* (Phyllodactylidae) of Gekkotabased on 12 dry skulls. Variation within each of these two taxa is discussed and compared. *Eublepharis angramainyu* displays several peculiar traits, such as stout and large braincase bones, a pair of small supratemporals, a solid parietal, and a pair of very small lacrimals. These elements are mostly absent in *A. elisae*. Further, there are differences in the premaxilla, palatine, and vomer, as well as the number of teeth on the premaxilla and maxillae. The above-

mentioned differences between the two taxa are mostly attributed to phylogenetic processes governing these two different evolutionary lines (Eublepharidae versus Phyllodactylidae).

Key words: *Eublepharis angramainyu*; *Asaccus elisae*; skull elements; comparative osteology.

1. INTRODUCTION

Most complicated of all reptilian skeletal structures and most important in problems of classification and phylogeny is the skull (Romer, 1956), and comparative anatomy of the skull between different taxa of lizards or in special species of lizards has always fascinated biologists (i.e. Häupl, 1980;Herrel et al., 1999; McBrayer, 2004; Bell et al., 2003; Stayton, 2005; Faizi and Rastegar-Pouyani, 2007, Conrad, 2008; Evans, 2008; Wise and Russell, 2010).

The Gekkota is one of major infraorders of lizards with more than 25% of all living genera and species of the lizard. Based on evolutionary models the diverse groups of Gekkota lizards (Pyron et al., 2013) encompass more than 108 genera 1500 species distributed principally in tropics and southern subtropics (Jonniaux and Kumazawa, 2008;Bauer, 2009; Gauthier et al., 2012).

The Gekkota have a short skull; temporal and postorbital arches absent; the jugal reduced and often rudimentary; no parietal foramen (Romer, 1956). A complete supratemporal arch, as well as an open supratemporal fenestra, is characteristic of most gekkotan lizards, including the Jurassic gekkotans (Romer, 1956; Kent and Miller, 2000). In the course of evolution the cranial bones reduced in number leading to intermixture of adjacent ossification centers, reduction or absence of ossification centers, and disappearance of sutures in young animals (Kent and Miller, 2000). The skull structure confirms this hypothesis as the numbers of skull bones in the more primitive *Eublepharis* are more than those of *Asaccus*.

The genus *Eublepharis*forms a natural group of nocturnal terrestrial Old World geckos ranging from southwestern Asia, and including five valid species: *Eublepharis angramainyu* Anderson and Leviton, 1966; *E. macularius*(Blyth, 1854); *E. turcmenicus*Darvesky, 1977, *E. hardwickii* (Günther, 1874) and *E. fuscus*(Börner, 1981). The range of this genus extends from southeastern Anatolia, Turkey, Iran, Iraq, Turkmenistan, Afghanistan, Pakistan, also eastern and western India. The leopard gecko, *E. angramainyu* was originally described from an old road between Masjed-Suleiman and Batwand, Khuzestan Province, Iran in 1966 by Anderson and Leviton. *E. angramainyu* occurs in the western foothills of the Zagros Mountains and in the upper Tigris-Euphrates basin in Iran, Iraq, southeastern Anatolian Turkey and northeastern Syria (Grismer, 1988; Anderson, 1999; Üzüm et al., 2008; Karamiani and Rastegar-Pouyani, 2010). The genus *Asaccus* Dixon and Anderson, 1973 (formerly included in *Phyllodactylus*Gray, 1828) is distributed in some parts of the Middle East region (Anderson, 1999; Rastegar-Pouyani, 2006).In 1973 Dixon and Anderson described a new species and genus of gecko from an unidentified locality around Islamabad, Kermanshah Province, and western Iran (Anderson, 1999). The genus *Asaccus* including at least 10 currently recognized species of leaf-toad geckoes distributed in northeastern Arabia (Oman, U.A.E), Zagros Mountains (Iran, Iraq). *Asaccus elisae*is widespread, extending into Turkey and Syria (Papenfuss et al., 2010). This paper has two major aims: The first is to present a detailed anatomical description of the head skeleton of *E. angramainyu* and *Asaccuselisae* discussing some osteological characters, and the second is to determine if there are additional skull characteristics attributable to the miniaturization process beyond those that have been identified in more general studies such as the allometric reduction of the neurocranium. Hence, in the present study, variation and differences in various parts of the skull in the two studied gekkotan taxa (*E. angramainyu* and *A. elisae*) are discussed.

2. MATERIAL AND METHODS

The specimens used in this study were collected in the field during 2007-2009 in different localities in Kermanshah and Lorestan Provinces, western Iran. The skulls were prepared by clearing and staining techniques based on commonly-used protocols (Wassersug, 1976; Dingerkus and Uhler, 1977; Song and Parenti, 1995). Six specimens of *E. angramainyu* (Mean SVL 146.10 mm) (RUZM-EE10.3-8) and six specimens of *Asaccus elisae* (Mean SVL 48.45 mm) (RUZM-GA 11-16) were used in this study. Following preparation, the skulls were scanned and photographed in different views by a scanner model Genius (ColorPage HR7XSlim), a Dino-Lite model AM313, and a Wild HEERBRUGG Binocular Microscope, and labeled (RUZM-SEE10.3-8; RUZM-SGA 11-16) (see appendix).

3. RESULTS

Dermatocranium of *Eublepharis angramainyu* Anderson and Leviton, 1966

The cranium is composed of six single (premaxilla, frontal, parietal, sphenoid, basioccipital and supraoccipital) and 18 paired bones (maxillae, nasals, prefrontals, jugals, lacrimals, vomers, septomaxilla, palatines, pterygoids, ectopterygoids, epipterygoids, postfrontals, stapes, squamosals,supratemporal, quadrates, prootics, otooccipital).

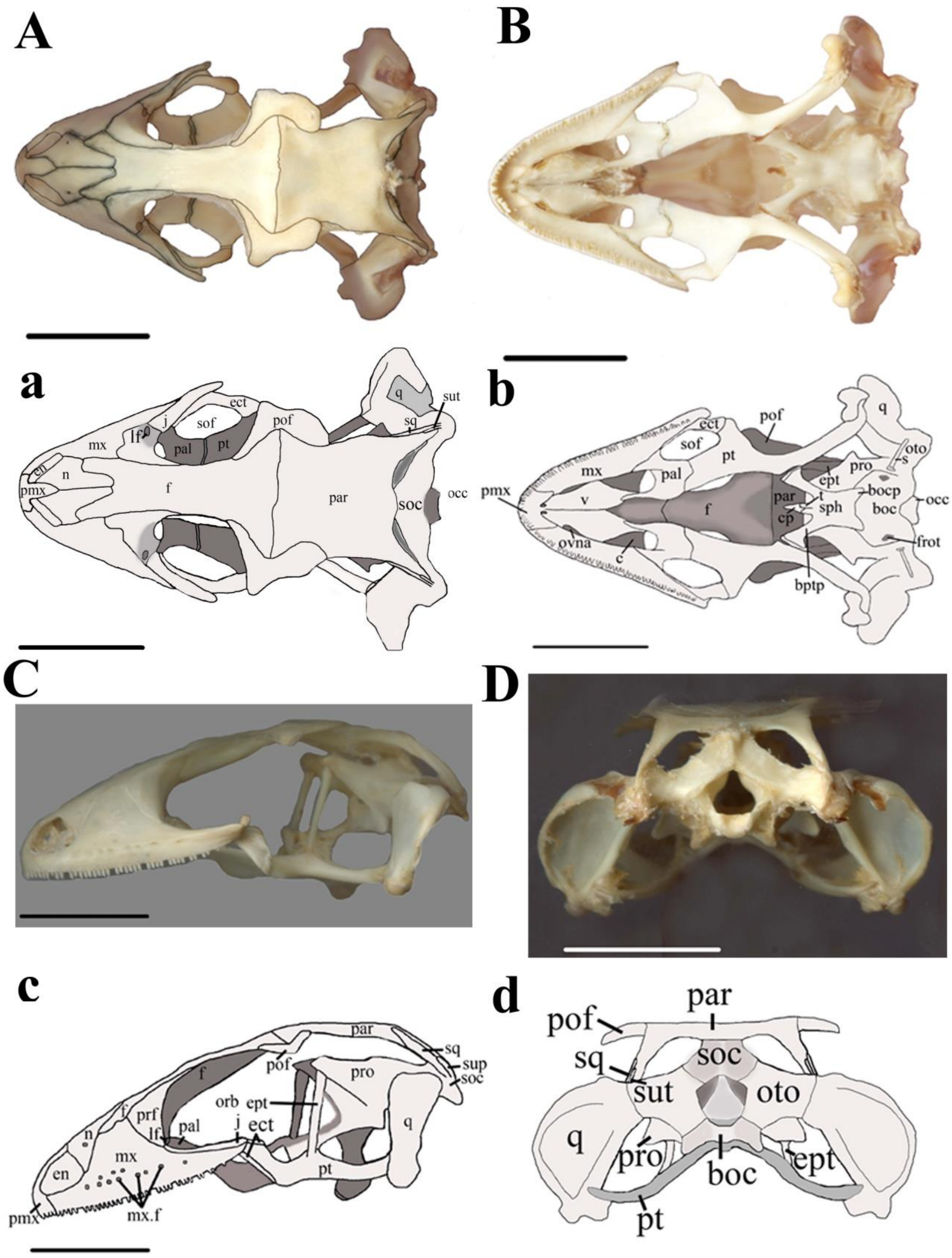

PLATE 1 *Eublepharis angramainyu* Anderson and Leviton, 1966.Skull in (A) dorsal, (B) ventral, (C) lateral, and (D) posterior view. Scans (a, b, c, d) and explanatory drawings (A, B, C, D). Scale bar = 10 mm. **Abbreviations:** boc, basioccipital; bptp, basipterygoid process; bocp, basioccipital process; c, choana;cp, cultriform process; ect, ectopterygoid; en, external nares; ept, epipterygoid; f, frontal; frot, foramen rotundum; j, jugal; lf, lacrimal foramen; mx, maxilla; mx.f, maxilla foramen; n, nasal; occ, occipital condyle; orb, orbit; oto, otooccipital; ovna, opening for the vomeronasal apparatus; pal, palatine; par, parietal; parp, paraparital; pmx, premaxilla; pof, postorbitofrontal; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; s, stapes; soc, supraoccipital; sof, suborbital fenestra; sph, sphenoid; sq, squamosal; sut, supratemporal; v, vomer; t, trabeculae.

Premaxilla (pmx)

This is an unpaired bone, T-shaped, forming the anteromedial margin of the snout and the medial margin of each fenestra exonarina, or external naris (Rieppel, 1981). The premaxilla (pmx) contacts the maxillae anterolaterally and anteroventrally; nasals posterodorsally, and vomerventromedially. The dorsal wide, convex, and ascending nasal process is arrowhead-shaped, and its ascending length 1.5 times the length of the dentary process, this process is roughly one-quarter the diameter of the external nares (Grismer, 1988) (Plate. 1A-C). In ventral view, the anteroventral border process forms anterior external nares, the palatal process forms the anterior edge of the medial foramen, the species has 14 functional teeth on premaxilla bone, the teeth are cylindrical, pleurodont, and have conical crowns.

Maxillae (mx)

These are large, paired, triradiate bones with anterior, dorsal (facial), and orbital processes occupying most of the anterolateral appearances of the skull between the fossa orbits and the snout, and orbital processes gradually becoming narrow towards the orbit. The maxillae contact the premaxillary processes anteriorly; the facial processes nasals anterodorsally, frontal dorsomedially, prefrontal posterodorsally, and the orbital processes contact jugalposteromedially, ectopteryogoid and palatine medially. In ventral view, it forms the posteroventral borders of the external naris and the lateral borders of both the internal naris and inner opening of the Jacobson's organ (Kluge, 1962). Eight to nine maxillary foramina (mx.f) are present on the lateral surface. These foramina are arranged in a nearly straight line that parallels the ventrolateral margin of each maxillary bone, in which there are three fossa posterolaterally (Plate. 1A-C).

Jugal (j)

These are paired, elongated, wedge-shaped and flat bones that are dorsal to the maxillae and extending beyond the posterior margin of the maxillae (orbital processes). The posterior process of the jugal is partially suspended, when the skull is viewed laterally. It contacts the dorsolateral region of the ectopterygoid, prefrontal and lacrimal anteriorly, being visible above the dorsal margin of the posterior maxillary process (Plate. 1A, C). Part of this bone projects posteriorly past the posterior end of the maxillary orbital process, the anterior portion much wider than the posterior portion (Grismer, 1988), it contacts the anterolateral and internal palatine, anterolateral external maxillary, and ectopterygoidventromedially.

Nasal (n)

This is a paired bone, convex anterodorsally, forming about 1/3 posterior margins of the external nares. It contacts the premaxillaryanteromedially, maxillae bone laterally, septomaxillaventromedially, frontal posteriolaterally, and with the other nasal medially, the anterior portion convex, wider than the posterior portion (Plate. 1A, C).

Frontal (f)

This is a single bone, hourglass-shaped, a median element forming the dorsal border of the orbits and the roof of the anterior region of braincase (De Queiroz, 1987). The ventral surface and the edges of the frontal become thick and round forming the supraorbital ridges, which meet on the midline, the tunnel formed by the ridge on theunderside (Plate. 1A-C). The frontal has two asymmetrical tips anteriorly, in which the right side is slightly longer. The frontal articulates with parietal posteriorly, postorbitofrontalposterolaterally, orbit fossa laterally, prefrontal and maxillae anterolaterally and nasal anteriorly.

Prefrontals (prf)

These are paired bones with concave bodies medially; they contact the frontal posteriordorsally, palatine posterioventerally, and the maxillae anteriomedially. In dorsal view, the prefrontal anterior portion forms the anterior margin of the orbit. The prefrontals articulate with the small lacrimal ventrally (Plate. 1A, C).

Lacrimal (l)

This bone is absent in most of the gekkotansbut when present is difficult to distinguish and may be overlooked (Daza and Bauer, 2010),These are paired bones, small, round, located between the lateral infraorbital processes of the prefrontal and the jugal, which sometimes is covered by the prefrontal; the lacrimals are barely visible by binocular stereomicroscope.

Palatines (pal). These are paired bones, contacting the vomer, maxillae, prefrontal, pterygoid, and ectopterygoid. Viewed from the ventral side, the palatine bones have a foot-like process which contacts vomer anteriorly, and anterolateral projection process which

contacts the maxilla. The palatine bone is greatly concave anteriorly where it forms the posterior and medial limits of the internal naris (De Queiroz, 1987). It forms the posterior border of the choana, the anterolateral border of the suborbital fenestra and the anteromedial border of the orbital fenestra (Plate. 1B, C).

Vomers (v)

These are paired bones, articulated with premaxilla anteriorly, maxillae anterolaterally and laterally, and with the other vomer medially, the septomaxilla dorsally and vomer posterior process contacts palatine. In between vomer and maxillae is a fossa, which is called the edge opening for the vomeronasal apparatus (ovna) (Daza et al., 2008), the vomer forms the floor of vomeronasal apparatus and also forms the anterior portion of roof of the mouth. The medial foramina are between the anterior edge vomers and posterior premaxilla. The posterior edge ofvomers associated with anterior edge palatine form the anteromedial edge of the choana (c), the posterior edges V-shaped.

Pterygoids (pt)

These are Y-shaped paired bones, the largest bones of the skull, contact the palatine, ectopterygoid and quadrate ventrally, and articulate with the basipterygoid process (bptp) of the sphenoid bone medially. It dorsally has a groove for connection with the epipterygoid; the anterior edge of the pterygoid is sinuous and connects the basal palatine bone (Plate. 1A, C).

Quadrates (q)

These are large, convex, paired bones forming posterolateral element of the skull, the base of articulation between the cranium and low jaw contact the squamosal and supratemporal dorsally, pterygoidventrointernally, and otooccipitaldorsomedially(Plate. 1A, C).
Septomaxilla (sm). These are paired, thin, small and convex bones. They lie in the nasal capsules and contact the premaxilla anteriorly and the maxillae posteriorly.

Ectopterygoids (ecp)

These are almost crescent-shaped, paired bones that contact the maxillae anterolaterally, palatine anteriorly, jugaldorsolatrerally and pterygoidposterolaterally. They complete the whole lateral border of suborbital fenestra, and part of the lateral margin of the inferior orbital foramen. Each ectopterygoid has two branches posteriorly, forming a y-shaped bone which completes the groove made by the short process of the pterygoids (Plate. 1A-C).

Postorbitofrontal (pof)

There is a single bone at the posterodorsal corner of the orbit (Daza and Bauer, 2010), these are paired, L-shaped bones, which articulate with inner margin of the frontal and the parietal, having a 110 internal angle. The anterior process contacts the frontal anteromedially and posterior process articulates the parietal posteromedially, forming a lateral brace for the movable frontoparietal suture (Rieppel, 1984). The posterior process is more expanded than the anterior process; the end of the anterior process is round (Plate. 1A, C).

Parietal (par)

This is an azygous and flattest bone of the skull, square-shaped with long posterior lateral processes, and each posterior process is overlapped by squamosal and supratemporal. The parietal bone contacts the frontal anteriorly, postorbitofrontalanterolaterally, prooticlaterodorsally, squamosal and supratemporalposterolaterally and supraoccipitalposterormedially (Plate. 1A, C).
Squamosal (sq). These are barb-shaped, paired bones contacting process of the parietal dorsoanteriorly, the prooticposteroventrally and the otooccipital and supraoccipital posteriorly (Plate. 1A, C, D).

Supratemporals (sut)

These are small, thin, paired bones, contacting the process of the parietal anterolaterally, squamosal laterally, and otooccipital posteriorly and may reach to quadrate;the supratemporalascended tohalfof the squamosal (Plate. 1A, C, D).

Epipterygoid (ept)

These are columnar-shaped, paired bones, extending from the pterygoid fossa middle to the crista alaris of the prootic bone, tilted posteriorly, and forming about 75˚ angle with the horizontal quadrate process of the pterygoids (Plate. 1C).

Stapes (s)

These are paired bones forming the columellaauris. Each bone consists of an oval foot plate which fits into the fenestra ovalis, and a laterally directed rod shape, which has a foramen at the base of the columella; it is the passageway of the stapedial artery (Rieppel, 1984) (Plate. 1B).

Prootics (pro)

This is a paired and irregularly-shaped bone, forming the anterodorsal wall of the braincase, and houses the anterior section of the membranous labyrinth (Kluge, 1962); it contacts the epipterygoidanterodorsally, sphenoid anteroventrally, the basioccipitalposteroventrally, supraoccipital dorsally, and the otooccipital posteriorly. It does not contact the parietal or the quadrate. The dorsal surface of the prootic is flat; the anterior portion forms dorsal alar processes. The prootic, associated with the otooccipital, houses the inner ear. It also forms the anterior margin of the fenestra ovalis (Daza et al., 2008) (Plate. 1B-D).

Supraoccipital (soc)

This is a butterfly-shaped bone which forms the posterodorsal margin of the braincase. It contacts the prootic anteriorly, and the otooccipitals ventrally, and forms the dorsal border ofthe foramen magnum (Kluge, 1962; Torres-Carvajal, 2003; Daza et al., 2008) (Plate. 1D).

Otooccipital (oto)

The otooccipital bone forms the posterolateral portion of the braincase, and the lateral rim of the foramen magnum. It articulates with the prootic anteriorly, with the basioccipitalventromedially, and the supraoccipital dorsally. It contacts the quadrate laterally, the parietal process, the squamosal, and the supratemporaldorsolaterally; in posterolateral view of the otooccipital the horizontal semicircular canal is visible. The occipital recess is located lateroventerally, is rectangular with rounded edges, and the fenestra ovalis. The occipital is surrounded by the otooccipital. There are three small foramina located posterior to the occipital recess, two of them as hypoglossal foramina, the larger fossa are the vague foramen which marks the original separation of the opisthotic and exoccipital (Bever et al., 2005; Daza et al., 2008) (Plate. 1D).

Occipital (oc)

This single bone consists of two parts: the first part is the basioccipital which is a centrally located element forming the posterior portion of the braincase floor, a shield-shaped bone which articulates the sphenoid anteriorly, prooticanterodorsally, otooccipital laterally and the occipital condyle posteriorly; the second part is the occipital condyle (occ), articulated with the first neck vertebra (Plate. 1B, D).

Sphenoid (sph)

This is an azygous, irregularly shaped compound bone thatis composed of the basisphenoid and tightly fused to the parasphenoid (Bever et al., 2005; Daza et al., 2008). The trabeculae (t) are located in the medial portion of sphenoid, which is strongly in contact with the prooticanterodorsally and the basioccipital posteriorly, and pterygoidanterolaterally. The anterior portion of the sphenoid forms the anterior portion of the cranial floor. The basiptrygoid process (bptp) is directed toward the pterygoids, and between those in the middle line; the trabeculae are symmetrical. The parasphenoid (pshd) rostrum islocated in the middle of the trabeculae that are supported by the cartilage of the cultriform process (cp) (Plate. 1B).

Mandible

Dentary (d)

The dentary is a tubular bone with the Meckelian canal closed, and bearing teeth on the inner dorsal margin (Kluge, 1962; Estes et al., 1988; Albino, 2005). It forms more than anterior half of the length of the mandibular ramus and bears 44-46 teeth (cylindrical, pleurodont, and with rounded crowns), which appear alternately and without spaces between them on a well-defined alveolar shelf. It contacts the coronoid dorsoposteriorly, the angular ventrally, the surangularexo- posteromedially, and splenialendo-posteromedially; the dentary bone has no articulation with articular. It forms ventral edge of seven dental foramina which are parallel the level of the medially -located crista dentalis (Kluge, 1962) (Plate. 2A- C).

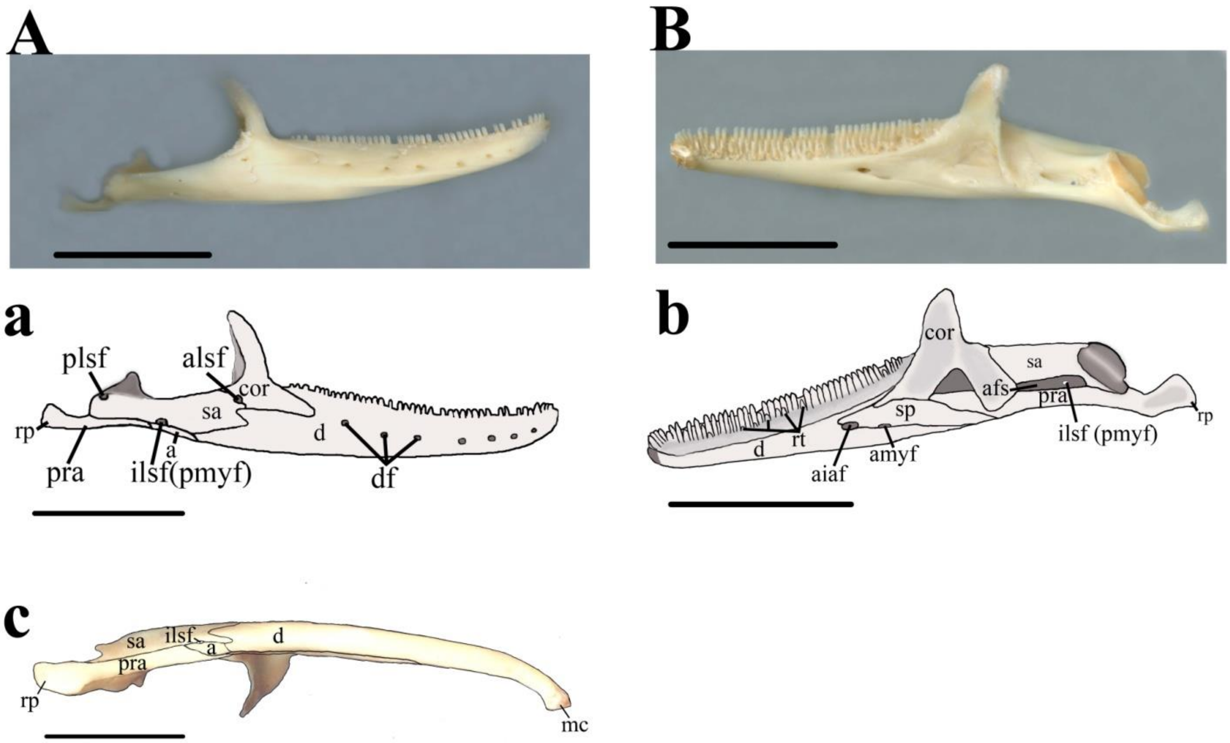

PLATE 2 Lower jaw of *Eublepharis angramainyu* in (A) lateral, (B) medial and (C) ventral view, Scans (a, b), explanatory drawings (A, B) and drawings on scan (c). Scale bar = 10 mm. **Abbreviations:** a: angular; cor: coronoid, d: dentary; afs, adductor fossa; aiaf: anterior; inferior alveolar foramen; amyf: anterior mylohyoid foramen; ap, angular process; df: dentary foramina; ilsf, inferiorolateralsupra-angular foramina; plsf, posterolateralsupra-angular foramina; pmyf, posterior mylohyoid foramen; pra, perarticular; mc, Meckel's cartilage; rp, retroarticular process, rt, repair teeth; sa: surangular, sp, splinal.

Coronoid (cor)

The coronoid lies immediately behind the mandibular tooth row (Torres-Carvajal, 2003). It is a triangular element that contacts the dentary anteriorly and the surangular posteriorly. At the inner surface of the mandible the coronoid consists of two processes: 1) the anterior inner process which is overlapped by the dorsal posterior portion of thedentary and the splenial. This process expands along the 14teeth on dentary and 2) the posterior inner process which overlaps the surangular, the anterior border of the adductor fossa, and the prearticular(Plate. 2A, B).

Surangular (sa)

The surangularforms the posterior half of the mandible and contacts the coronoid and dentary anteriorly, the angular ventrally, borders the adductor fossa dorsally, and prearticularposteriorly. The surangular contains three foramina: (1) the more dorsally located posterolaterallysurangular foramen (plsf), (2)the posterior mylohyoid foramen (pmyf) located between the angular and surangularventrally, and 3) the anterolateral surangular foramen (alsf) located between coronoid and surangularanteromedially (Plate. 2A- C).

Angular (a)

The angular is the smallest and the thinnest bone of the mandible, the angular more is visible surfaces ventrally. It overlaps lateraloanteriorly of the surangular, lateraloposteriorly of the perarticular, and lateroanteriorly of the dentary and the splenial (Plate. 2C).

Splenial (sp)

The splenial is the bone only visible that is located on the inner, medial, and ventrolateral aspects of the mandible. It articulates with the anterior process of the coronoid dorsally, the prearticularpostroventerally, the dentary anteriorly and dorsally. The splenial forms posterior margin of the anterior inferior alveolar foramen (aiaf), and in whichlies the anterior mylohyoid foramen (amyf) (Plate. 2B, C).

Prearticular (pra)

The prearticular forms the posterior end of each mandibular ramus in medial aspect. On its posterior surface it bears two processes: the retroarticular process (rp) posteriorly and the angular process dorsomedially, which contain the area for articulation with the quadrate. The prearticular is fused with the articular dorsally. In lateral view, the prearticular contacts the angular anteriorly, and the suprangularanterodorsally (Plate. 2A- C).

Marginal teeth (mt)

All the teeth are conical pleurodont type, and are located in the inner wall of the mandible in varying sizes and stages of replacing the adult teeth. The premaxillary bears 14 pleurodont teeth of about 6.3mm length each, and the maxillary teeth range from40- 44 pleurodont teeth with rounded crowns (Plate. 4F).

Dermatocranium of *Asaccus elisae* (Werner, 1895)

Skull depressed, flat and broad, dermal bones thin; pterygoids flange (Romer, 1956). The cranium consists of five single bones (premaxilla, frontal, sphenoid, basioccipital and supraoccipital) and 17 paired bones (maxillae, nasals, parietals, prefrontals, jugals, vomers, septomaxilla, palatines, pterygoids, ectopterygoids, epipterygoids, postfrontals, stapes, squamosals,quadrates, prootics, otooccipitals) (Plate. 3A- D).

Premaxilla (pmx)

This is a small, unpaired element forming anteromedial margin of the snout and the medial margin of each fenestra exonarina, it overlaps the maxillae anterolaterally and anteroventrally; nasals posterodorsally, and vomerventromedially (Plate. 3A- D).

Maxillae (max)

This is large and triradiate, the maxilla articulates with the premaxillary processes anteriorly, the facial processes of nasals anterodorsally, frontal dorsomedially, prefrontal posterodorsally, and the orbital processes contact jugalposteromedially, ectopteryogoid and palatine medially. In lateral view, 6-7 maxillary foramina (mx.f) are visible (Plate. 3A- D).

Jugal (j)

This is a small, thin, short, wedge-shaped and flat bone; that is located dorsal to the maxillae and extends beyond the posterior margin of the maxillae (orbital processes) (Plate. 4A).

Nasal (n)

The nasals contact the premaxillary process anteriorly and edges roughly with the process of the frontal posteriorly, forming roof of external nares and the nasal capsules, maxillae laterally, and septomaxillaventromedially, does not have contact with the prefrontal, and a medial contact with the other nasal (Plate. 3A- D).

Frontal (f)

The frontal contacts the nasal anteriorly, maxillae anterolaterally, has a small contact with the prefrontal laterally, forming the dorsal border of the orbits, postorbitofrontalposterolaterally, and parietals posteriorly. The lateral processes are slender and smaller than the median process.

Prefrontal (prf)

This is a crescent-shaped bone that contacts the frontal posteriordorsally, palatine lateroventerally, and the maxillae anteromedially and infraorbital foramen ventralaterally. In dorsal view the anterior portion of prefrontal forms the anterior margin of the orbit.

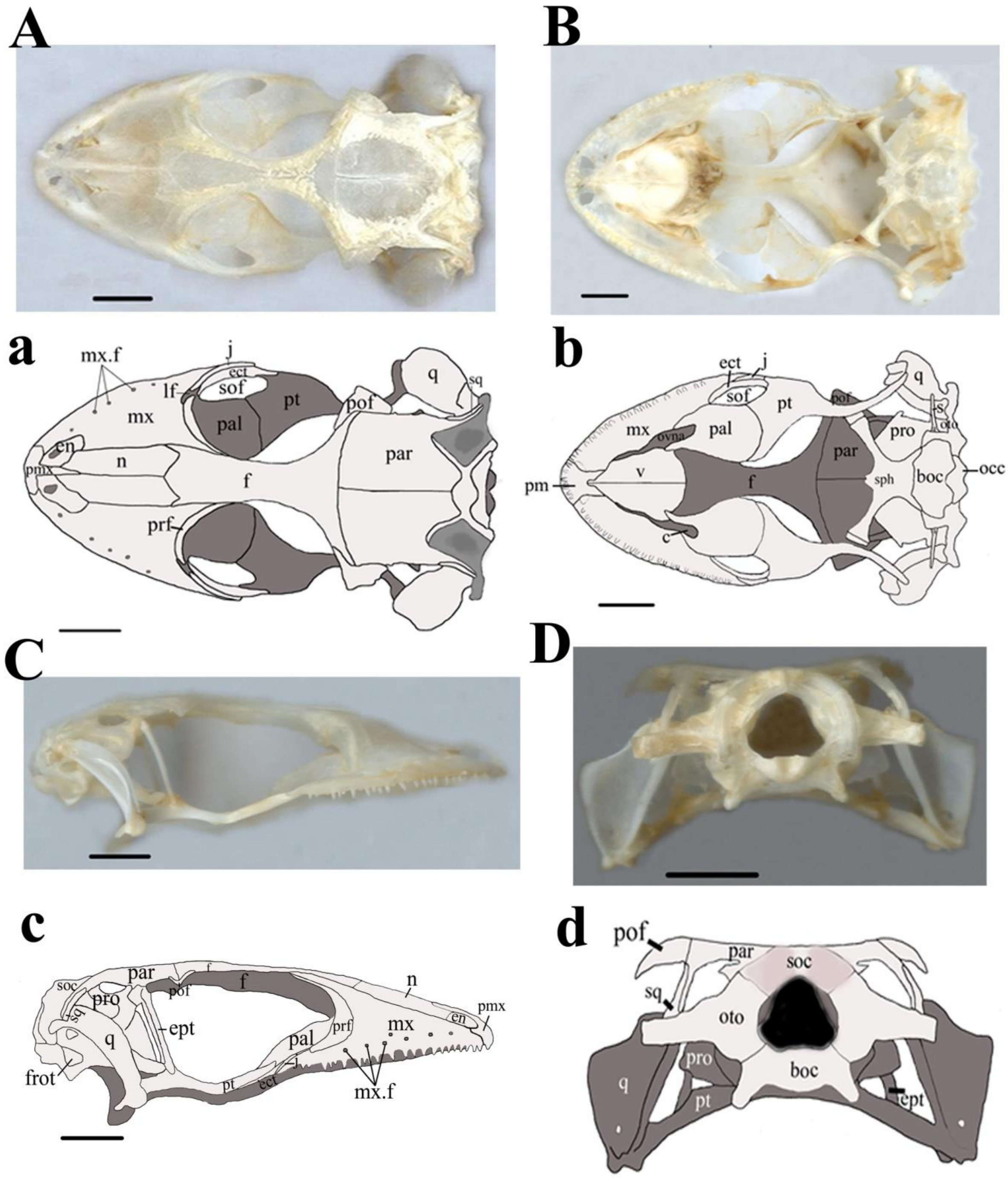

PLATE 3 *Asaccus elisae* Werner, 1895. Skull in (A) dorsal, (B) ventral, (C) lateral, and (D) posterior view. Scans (a, b, c, d) and explanatory drawings (A, B, C, D). Scale bar = 2 mm. **Abbreviations:** boc, basioccipital; c, choana;cp, cultriform process; ect, ectopterygoid; en, external nares; ept, epipterygoid; f, frontal; frot, foramen rotundum; j, jugal; lf, lacrimal foramen; mx, maxilla; mx.f, maxilla foramen, n, nasal; occ, occipital condyle; orb, orbit; oto, otooccipital; ovna, opening for the vomeronasal apparatus; pal, palatine; par, parietal; pmx, premaxilla; pof, postorbitofrontal; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; s, stapes; soc, supraoccipital; sof, suborbital fenestra; sph, sphenoid; sq, squamosal; v, vomer.

Lacrimals (l)

The lacrimals are absent in *Asaccus elisae*.

Palatine (pal)

The palatine contacts vomer anteriorly, and anterolateral projection of its process contacts maxillae, it forms the posterior border of the choana, the anterolateral border of the suborbital fenestra and the anteromedial border of the orbital fenestra.

Vomers (v)

These are paired bones, contacting premaxilla anteriorly, maxilla anterolaterally, and with the other vomer medially, the septomaxilla dorsally, and palatine posteriorly. The vomer forms the floor of vomeronasal apparatus also the anterior portion of the oral roof. The medial foramina are very small. The posterior edge of the vomers with associated anterior edge of the palatine form the edge of the choana (c). The posterior edges concave.

Pterygoids (pt)

The pterygoids are the largest bones of the skull, Y-shaped, contacting the palatine, ectopterygoid and quadrate ventrally, and cartilaginous pterygoid meniscus of the basipterygoid process of the sphenoid bone. On the dorsal surface it contacts the epipterygoid, and the anterior edge is concave and contacts basal palatine bone.

Quadrates (q)

The quadrates are large, convex posterolateral elements on the skull that contact the squamosal dorsally, otooccipitaldorsomedially, pterygoidposteromedially; the inner surface of the quadrate has a convex, smooth anterior surface and partly concave posterior space for the auditory meatus. Thispart has no muscles for its closure in geckonids similar to sphaerodactylids (Bernstein, 1999; Daza et al., 2008), providing a channel for inner ear.

Septomaxilla (sm)

The septomaxillae are thin and membranous,covering the vomeronasal apparatus dorsally (syn. organ of Jacobson) as in most Squamata and contact the maxillae anterolaterally and the vomers ventrally.

Ectopterygoid (ecp)

In ventral surfaceit contacts the maxillae anterolaterally and palatine anteriorly. In dorsal view, it is articulated with the jugaldorsolaterally and pterygoidposterolaterally. It makes the lateral border of suborbital fenestra, and part of the lateral margin of the inferior orbital foramen (Plate. 4B).

Postorbitofrontal (pof)

The posorbitofrontals are L-shaped bones that contact the margin of the frontal and the parietal, and have a 100º internal angle. The anterior process of postorbitofrontal contacts the frontal anteromedially and the posterior process articulates the parietal posteromedially, forming a lateral brace for the movable frontoparietal suture (Rieppel, 1984) (Plate. 3A- D).

Parietal (p)

These are paired and flattest bones of the skull, square-shape with long lateral processes posteriorly, and contacting the frontal anteriorly, postorbitofrontalanterolaterally, prooticlaterodorsally, squamosal posterolaterally and supraoccipitalposterormedially, and a medial contact with each other (Plate. 3A- D).

Squamosal (sq)

The squamosals are slender barb-shaped bones that contact the process of the parietal dorsoanteriorly, the prooticposteroventrally and the otooccipital and supraoccipital posteriorly (Plate. 3A- D).

Supratemporal (st): Absent.

Epipterygoid (ept)

This is a paired bone; rod-shaped, extending from the pterygoid fossa middle to the crista alaris of the prootic bone, slightly tilted posteriorly, forming a pair of vertical braces between the palate and the skull (Torres-Carvajal, 2003), each ectopterygoid forming a 73° angle with the horizontal quadrate process of the pterygoid. The epipterygoidlengthisabout 3.25mm (Plate. 3A- D).

Stapes (s)

This is a paired bone forming the columellaauris. Each stapes consists of an oval foot plate which fits into the fenestra ovalis, and a laterally directed rod shaped process, the stapes bone has a foramen at the base of the columella, and articulates by a cartilaginous connecter with the quadrate (Plate. 4C).

Prootic (pro)

The prootics form theanterodorsal wall of the braincase, and contact the epipterygoidanterodorsally, sphenoid anteroventrally, the basioccipitalposteroventrally, supraoccipital dorsally, and the otooccipital posteriorly.

Supraoccipital (soc)

The supraoccipital forms posterodorsal margin of the braincase and the dorsal border ofthe foramen magnum dorsally, and contacts the prootic anteriorly, and the otooccipitals ventrally, and parietal dorsally.

Otooccipital (oto)

The otooccipital bone forms posterolateral portion of the braincase, and the lateral border of the foramen magnum. It articulates with the prootic anteriorly, with the basioccipitalventromedially, the supraoccipital dorsally. Each otooccipital has a horizontal process that contacts the quadrate laterally, and with the parietal process and the squamosal dorsolaterally.

Occipital (oc)

The occipital is unpaired, includes the occipital condyle posteriorly and the basioccpital bone that is a centrally-located element forming the posterior portion of the braincase floor, contacting the sphenoid anteriorly, the prooticanterodorsally and otooccipitaldorsolaterally (Plate. 3B, D).

Sphenoid (sph)

The sphenoid bone contacts the prooticanterodorsally, the basioccipital posteriorly, and pterygoidanteriolaterally. In the anteriomedial portion it bears a pair of cartilaginous rods which were separated during skull preparation (Plate. 3B).

Mandible

Dentary (d)

The dentary is a tubular bone with the Meckelian canal closed, and bearing teeth on the inner dorsal margin. It forms more than half of the anterior length of the mandibular ramus and bears teeth. The dentary contacts the coronoid dorsoposteriorly, the surangular on outer posteromedially, and splenial on the inner posteromedially. In the outer surface it has five dental foramina at the medial level (Plate. 4D- E).

Coronoid (cor)

The coronoid bone contacts the dentary anteriorly, and the surangularposteroventrally. It contacts the splenial anteriorly, and the compound bone (cob) anteroventrally in the inner surface (Plate. 4D, E).

Surangular (sa)

The surangularforms the posterior half of the mandible and contacts the coronoid, dentary anteriorly, and the compound bone posteriorly; also it bears the mandibular fossa (mf).The surangular contains two foramina: the first anterolateral surangular foramen (alsf) located on its dorsal border, and second posterolateralsurangular foramen which is located in the posterolateral surface of the surangular (plsf) (Plate. 4D).

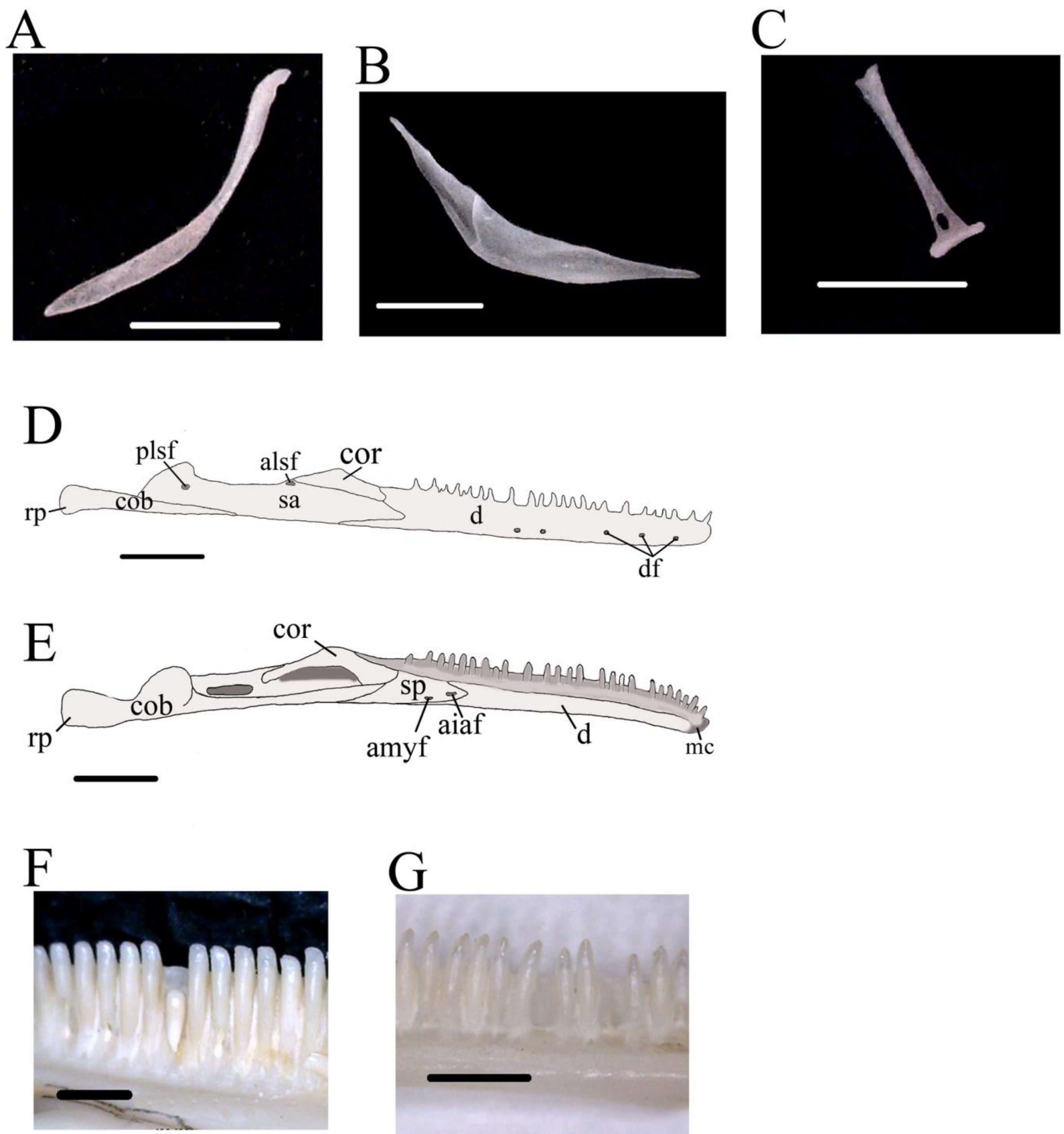

PLATE 4 Jugal, **B**: ectopterygoids and **C**: stape in *Asaccus elisae* Werner, 1895 photography with Dino Capture. Scale bar = 1mm; Lower jaw of *Asaccus elisae* Werner, 1895 in (**D**) lateral and (**E**) medial, explanatory drawings. Scale bar = 2 mm. **Abbreviations:** a: angular; cob, compound bone; cor: coronoid, d: dentary; afs, adductor fossa; aiaf: anterior; inferior alveolar foramen; amyf: anterior mylohyoid foramen; df: dentary foramina; ilsf, inferiorolateralsupra-angular foramina; plsf, posterolateralsupra-angular foramina; pmyf, posterior mylohyoidforamen;para, retroarticular process; mc, Meckel's cartilage; rp, retroarticular process; sa: surangular, sp, splinal. Comparison teeth of middle dentary in (**F**) *Eublepharis angramainyu* and (**G**) *Asaccus elisae* Scale bar= 1mm

Angular (a)
The angular is absent.

Splenial (sp)
The splenial bone is located in the inner mandible and contacts the anterior process of the coronoid dorsoposteriorly, the compound bone (cob) posteriorly and the dentary anteriorly. The splenial bears two foramina:the anterior inferior alveolar foramen (aiaf), and the anterior mylohyoid foramen (amyf) (Plate. 4E).

Compound bone (cob)

The compound bone (prearticular + articular)forms the posterior end of each mandibular ramus in medial aspect. Because of fusion of prearticular and articular in adults, these bones are described together. The compound bone contacts with the surangular and the splenial anteriorly (Plate. 4D, E).

Marginal teeth

All the teeth are conical, pleurodont type, and are located in the inner wall of the mandible in varying sizes and stages of replacing the adult teeth. The premaxillary bears 10-12 pleurodont teeth and the maxillary teeth range from 34-36, for each side and the dentary bears 27-35 cylindrical, pleurodont teeth with sharp crowns, appearing alternate and without space on a well-defined alveolar shelf (Plate. 4G). The measurements of skull characters in *Eublepharis angramainyu* and *Asaccus elisae* are given in Table 1.

Table 1 Measurements of the skull characters (in millimeter) in *Eublepharis angramainyu* Anderson and Leviton, 1966 and *Asaccus elisae* (Werner, 1895).

Characters	Taxon		Description
	E. angramainyu	***A. elisae***	
Skull length	35.26	14.88	From the anteriormost part of the premaxilla to the space between the divided occipital condyle
Skull greatest width	18.16	7.78	Between the most lateral part of the quadrates
Premaxilla length	6.66	2.55	From the anteriormost part of the premaxilla to the posterior end of the ascending nasal process
Premaxilla width	5.2	1.90	From each premaxilla–maxilla suture
Width between the jugals	1,01	0.14	Measured between the posterior end of the jugals
Frontal posterior width	10.53	4.77	Measured at the posterior end of frontal
Width the postorbitofrontals	1.54 / 2.34	0.28 / 0.73	Width of anterior portion / posterior portion each postorbitofrontal
Maxilla length	17.7	7.73	From the premaxilla–maxilla suture to the end of the posterior process of the maxilla
Occipital condyle width	2.03	0.75	Across the divided occipital condyle
Orbit length	11.04	5.59	From the anteriormost margin of the orbit to the vertices of the postorbitofrontal
Highest point of the skull	13.35	4.18	From the mandibular condyle to the skull roof
Jaw length	34.77	15.74	From the mandibular symphysis to the posterior end of the retroarticular process of the left ramus
Height of the jaw	8.89	1.04	At the level of the coronoid
Jaw tooth row	17.12	8.21	Length of tooth-bearing portion of mandible
Stapes length	3.01	1.5	Length of stapes
Epiptrygoid	7.39	3.25	Length of epiptrygoid

4. DISCUSSION

The vertebrate head is an example of a complex integrated system, where one function cannot be optimized without potentially compromising others (Herrel et al., 2001). The comparative anatomy of the skull between different taxa of lizards for answering questions such as structure of the skull and differences and origin of these differences between lizards has always fascinated biologists, and hasbeen a major information gathering and processing center for immensely diverse functions, such as feeding, breathing, drinking, display, and in many tetrapods also vocalization, have to be performed by the same elements.

The first difference that is apparent in the skulls of the two above-mentioned taxa is the differences in the head width/ head length ratio: in *Asaccus elisae* this ratio is about 0.63 whereas in *Eublepharis angramainyu* it is about 0.8, and in the head width/ head height ratio: in *Asaccus elisae* this ratio is about 2.42 whereas *in Eublepharis angramainyu* it is about 0.23, therefore the skull in *Asaccus elisae* is relatively wide in comparison to that of *Eublepharis angramainyu*, because they are adapted to live on cave ceilings, under flakes of exfoliating rock, and in culverts, so greater head -size should be an advantage for feeding. But in *Eublepharis angramainyu* the habitat is characterized by gypsum hills and arid grasslands, and it often occurs in the small caverns in the gypsum deposits. Other differences between these two taxa are as follows: *Eublepharis angramainyu* has 18 paired bones in skull with a single parietal, while in *Asaccus elisae* there are 17 paired bones and parietals are paired. *Eublepharis angramainyu* has a pair of small lacrimal bones as well as a pair of thin and small supratemporals, but these bones are absent in *Asaccus elisae*. All the teeth in the two taxa are conical, pleurodont, and almost similar, but*Eublepharis angramainyu*has 14 premaxillary teeth and about 40 to 42 maxillary teeth with rounded crowns, while*Asaccuselisae* has 10-12 premaxillary teeth and about 34-36 maxillary teeth with sharp crowns. These differences in the number and shape of teeth in the two taxa are indicative of use of different food items: *Eublepharis angramainyu* eats large specimens (solpugids, spiders and beetles) and small geckos while*Asaccus elisae* uses small insects in its diet (mosquitos, flies, ants etc.).

In *Eublepharis angramainyu* the anterior portion of the nasal is wider than the posterior part which overlaps with the anterior part of the frontal, whereas in *Asaccus elisae* the anterior and posterior parts of the nasal are almost equal in width, and posterior processes have a regression so that the anteriomedial process of the frontal has filled the space between them.

Another difference in these two taxa is in the mid-line of the nasal length/ head length ratio so that in *Eublepharis angramainyu* it is 0.14 while in *Asaccus elisae* it is 0.2. The frontal in *Eublepharis angramainyu* bears two anterior processes which are continued until about 62.5% of the nasal length from the lateral view but in *Asaccus elisae* there are three processes in which lateral processes continue until about 11.7% of the lateral view of the nasal. Further, in *Asaccus elisae* the middle process of the frontal is present but in *Eublepharis angramainyu* this element is absent. In *Eublepharis angramainyu* the frontal contacts the parietal in a straight line, while the posterior portion of the frontal in *Asaccus elisae* is arc-shaped.

The parietal in *Eublepharis angramainyu* is a single bone whereas in *Asaccus elisae* it is paired with slender posterior processes. In *Eublepharis angramainyu* the middle portion of the vomer contacts the maxilla, and the posterior process is juxtaposed with the anterior process, while in*Asaccuselisae* the vomer only contacts maxillae anteriorly, and it does not have a posterior process. This may increase the cranial kinesis of the skull in *A. elisae*. The jugals are reduced and often rudimentary (Romer, 1956) in *Asaccus elisae* relative to *Eublepharis angramainyu*. In *Asaccus elisae* the internal angle between parasphenoid with the inner margin of the trabeculae is looser than that of *Eublepharis angramainyu*.In posterior view of the skull, differences appear between the two taxa in the shape of length of supraoccipital and occipital condyle so that in *Eublepharis angramainyu*the supraoccipital is shorter than that of *Asaccus elisae*.

One of the other main differences between the two taxa is the presence of the angular in *Eublepharis angramainyu* and its absence in *Asaccus elisae*. There are also differences in the inner surface of the jaw between the two taxa: in *Eublepharis angramainyu* 1) the superior process of the coronoid is prominent and the angle between the anterior inner process with the inner process of the coronoid is more narrow2) the anterior inferior alveolar foramen (aiaf), and the anterior mylohyoid foramen (amyf) are located between dentary and splenial, while in *Asaccus elisae* 1) the superior process of the coronoid is round, and the angle between the anterior inner process with the inner process of the coronoid is wider, 3) the splenial is surrounded by the anterior inferior alveolar foramen (aiaf) and the anterior mylohyoid foramen (amyf). But in the outer surface of the jaw: 1) the number of the dentaryforamina (n=7 for *Eublepharis angramainyu*, and n=5 for *Asaccus elisae*), 2) in *E. angramainyu* the anterolateral surangular foramen (alsf) is located between the surangular and the coronoid. In *A. elisae* the alsf is located more dorsally and more posteriorly. In*Eublepharis angramainyu* the posterolateral area of the surangular foramen (plsf) is located in the extreme posterior area of the surangular, while the same combination in *A.elisae* is located more dorsally and less posteriorly (Plate 2 and Plate 4D-E).

In *Eublepharis angramainyu* the posterior mylohyoid foramen (pmyf) is located ventrally between the angular and surangular whereas in *Asaccuselisae* the posterior mylohyoid foramen (pmyf) is clearly visible.

And finally, based on this study and with regards to the mentioned differences in various skull elements between the two studied taxa, and in concordance with Kluge (1967; 1987), we are now inclined to consider *Eublepharis angramainyu* and *Asaccus elisae* as belonging to two different families (Phyllodactylidaeand Eublepharidae).

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Appendix I

Material examine

1. Cutting head specimen.
2. Carefully detaching head skin and muscles.
3. Loading skulls in 15% sodium chloride solution for 24 hours (to dehydrate), and remove any remaining tissues.
4. Loading skulls in gasoline for 6-12 hours (to degrease).
5. Loading skulls in NaOCl (Sodium hypochlorite) 3% for 12-24 hours (to bleach).
6. Using H_2O_2 (Hydrogen peroxide) 3% for 6- 12 hours in complete darkness (complete bleaching).
7. Dehydrating skulls by depositing them in 96% ethanol.
8. Preparing photos by scanner.
9. Using Dino-Lite model AM313 and Wild HEERBRUGG Binocular Microscope, to study more details.
10. Drawing schematic skull elements.